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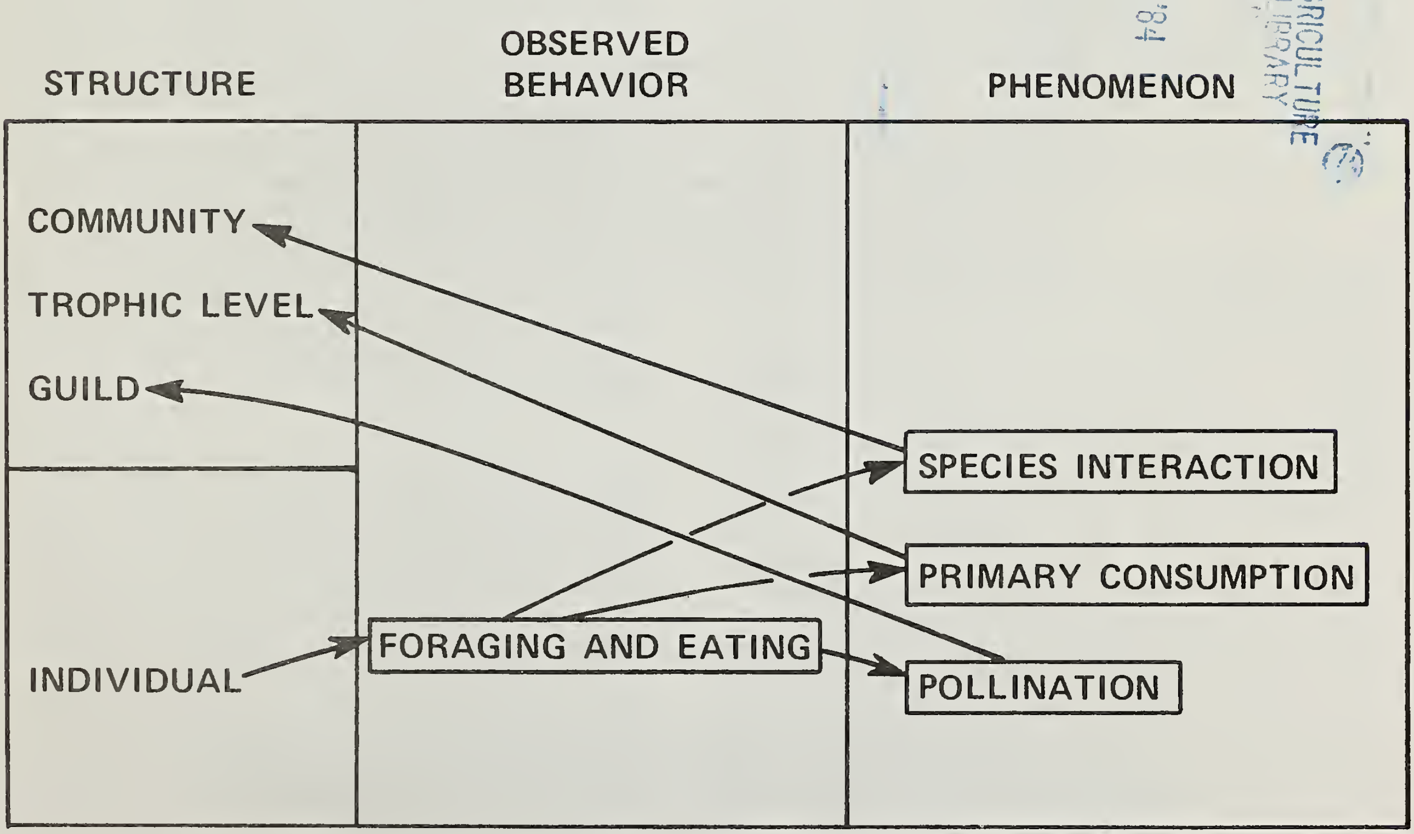
Interlevel Relations in Ecological Research and Management: Some Working Principles from Hierarchy Theory

T. F. H. Allen, R. V. O'Neill, and T. W. Hoekstra



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Interlevel Relations in Ecological Research and Management: Some Working Principles from Hierarchy Theory[1]

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Abstract

This report clarifies the role of the observer and what he observes as an aid to ecological research and natural resource management. It describes what is involved in observing complex natural systems, the role of the observer in moving through surfaces of natural systems, and finally summarizes, from these, the important principles in linking levels of natural systems that emerge.

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Introduction

Ecologists study complex systems which span many levels of organization (e.g., organisms, populations, and communities). As a result, ecologists face the difficult problem of linking levels of organization. Differences in criteria for organization and dynamic behavior make simple aggregation of lower levels insufficient to explain higher levels. What is needed is a set of working principles that allow the ecologist to keep track of terms and data between levels.

Although criteria for organization change between levels, there are consistent patterns that order interlevel relationships and perception of those relationships. For example observations made with coarser grain resolution will necessarily detect high levels of organization as long as observational criteria are held constant. Furthermore, this is true independent of which criteria are actually used for observation be they physiological, floristic, or hydrological. Also, sets of observation extending over larger areas and/or longer time will similarly be able to detect higher levels of organization. Thus, grain and extent are crucial to ordering perception of levels. Perception of higher or lower levels involves the passage of the ecological observer through what are functionally ecological surfaces. Surfaces are crucial to defining levels.

Ecologists often are faced with coupling the level that contains readily perceived objects (i.e., organisms) to other levels where there are valid but less tangible entities (e.g., ecosystems). Moving to lower levels sometimes demands observation of entities (e.g., microbes) and processes (e.g., stomatal opening) much smaller than ordinary human perception. Moving to higher levels of organization, the entities are also hard to perceive and several observations must be conceptually linked before the structure emerges.

Higher levels of organization are particularly troublesome. Ecologists have only recently possessed computational power commensurate with physically large systems. Inexperience with complex systems is sometimes brought home with unkind force, when dust bowls arrive in real time or when computer simulations produce absurdities. Nevertheless, society recognizes pressing problems precisely in these large scale systems, and it demands, quite fairly, that ecologists contribute to solutions. For example, the 1974 Forest and Rangeland Renewable Resources Planning Act requires that each decade the USDA Forest Service not only report on the status and trend of forest, wildlife, range, recreation, and fisheries resources at a national level, but also that it translate effects of local management practices into national level programs to support national needs. It seems to be ecology's responsibility to link small scale systems production estimates to production in large scale complex systems, but how to start?

Prior to the American effort in the International Biological Program, it was believed that ecological systems could be almost perfectly simulated, given enough electronic memory and sufficiently fine-grained data. Few would maintain that today. Apparently, there is more to complex systems than lots of little bits of information. Part of that "something more" may be found in the hierarchical organization that structures complex systems (Allen and Starr 1982).

This report examines general ways to study complex systems, and develops general principles pertinent to such problems. These principles are derived from a detailed analysis of what an observer of a complex system will experience, and the precautions that must be taken in linking levels of organization. While the principles have much generality, the focus is on complexity in systems of particular concern to ecologists.

Observing Complexity

Role of Surfaces

Two distinctions are needed to characterize a hierarchical system. First, there is the distinction between structural entities at a given level of organization (e.g., the distinction between two trees). Second, there is the distinction between successive levels (e.g., between trees and the forest). The two distinctions are related. On the level at which trees are distinguished, the interesting behavior involves how one tree interacts with another. At the "forest" level distinctions between trees are lost, but boundaries, such as forest edges, are recognized.

Hierarchies are, in the most general terms, partially ordered sets (Sugihara 1983) where there is an asymmetry of relationship between elements. Several criteria are particularly helpful for defining asymmetry in ecological hierarchies. These criteria define higher levels as (1) containing (in nested systems), (2) constraining, (3) the context of, (4) behaving at a lower frequency than, and (5) exhibiting less bond strength than, lower levels (Webster 1979).

The definition of any structure may be seen in terms of these criteria. A complex structure is made of smaller structures and is a component of a higher level of the hierarchy (fig. 1). The entity to be defined is contained by its outer surface (criteria 1-3). Surfaces in space are those places around which the strength of interaction is most variable. Inside a surface there is a collection of parts with strong interactions (criterion 5) and rapid exchange (criterion 4) (Simon 1962, 1973). Thus, surfaces define separate entities and are responsible for the characterization of discrete levels of organization (Allen and Starr 1982).

Now introduce an observer to see what effects surfaces have upon what is observed. Consider exchange across a surface that is weak and sluggish (Platt 1969). An observer inside the surface detects high frequency behavior associated with rapid exchanges among components (fig. 2). An observer outside sees slower behavior characteristic of interactions among higher level entities (fig. 3). Thus, the surface is defined by a change of frequency, sandwiched between high frequency behavior inside and low frequency exchanges outside. The relationship of the surface to the observer is crucial to determining what is observed.

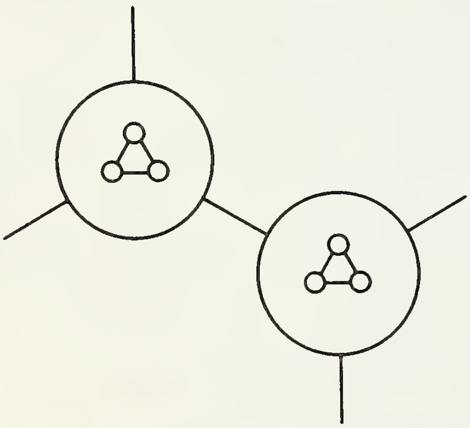

Figure 1.—A hypothetical system with various parts visible under different protocols for observation. The full system is composed of two entities, each with three parts. The complete system is not visible within any single observation set.

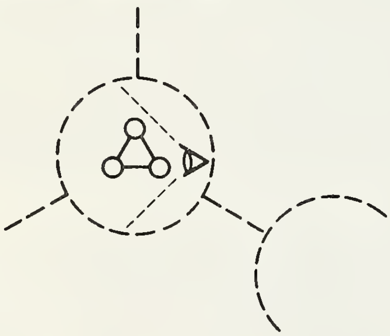

Figure 2.—Inside the surface, looking inward, is the only position from which the parts and their interconnections can be seen without distortion. (The eye indicates the position from which the system is observed.)

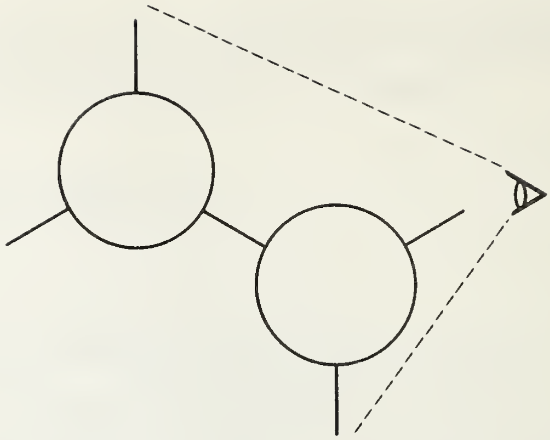

Figure 3.—If the observer moves far enough away from the surface, the other whole is identifiable as a separate entity, responsible for part of the environmental influence. (The eye indicates the position from which the system is observed.)

Relax the requirement that surfaces be situated in certain places in space, and the essential features remain; configurations that define observable entities can still be detected. For example, the Krebs Cycle can be distinguished as an entity, even though its enzymes, substrates and products all interdigitate with a mixture of other organic molecules. Similarly, cycling pathways may be detected in ecological nutrient data. The pathway is adequately defined by frequency characteristics even though the cycle cannot be mapped on the ground. It is the difference in reaction rates within, as opposed to without, that defines the entity (Levins 1973).

A critical characteristic of surfaces is their power of integration (Platt 1969; Simon 1962, 1973). Thus, for example, the surface of a community may be recognized by the way component biota are integrated into an interacting unit. The fact that this surface does not map easily onto a particular part of three-dimensional experiential space is, for present purposes, superfluous. This approach to surfaces provides a tool for dealing with levels where there are intangibles above and below the level of commonplace human experience. Discussion of surfaces, henceforth, will include these intangible surfaces as a normal case.

Observation Sets

Because of the importance of surfaces in distinguishing entities and levels of organization, researchers and managers must be explicit about how they look at an ecological system and detect the surfaces. The critical concept here is the observation set. An observation set defines how the investigator decides to look at a system. Two decisions are required. First, the investigator chooses the objects of study. He picks the level on which he will focus; this, in turn, determines the structural entities he will discriminate (Rosen 1977). In other words, the investigator must decide if he will look at cells, organisms, guilds, or communities. Second, the investigator must decide on the phenomena of interest. He chooses those changes in the objects of study which will

be considered as interesting (Pattee 1978). Thus, although he has decided to look at populations as his object of study, he must still decide whether he is interested in, say, the phenomenon of growth (i.e., changes in numbers through time) or migration (i.e., changes in numbers over space).

The observation set begins with a data set, but goes beyond just a collection of raw measurements. The observation set is the means to observe in a scientific manner. It is coupled to a procedure for collecting data, such as tree densities in 0.1-ha plots or flourometric readings of plankton chlorophyll. More than this, scientific observation involves methods of analysis such as Fourier transformation or ordination of binary transformed data. Observation also involves criteria for identifying significance (statistical or otherwise) in the results of analysis. Only when the raw data are analyzed and the significance of the analysis is recognized, is the critical role of observation complete. The observation set depends upon the scientist's paradigm (Kuhn 1962) and is deeply influenced by the way he considers his object of study.

A pH meter reading alone does not constitute an observation set because observation is not complete without fixing (1) the procedure for taking the readings, (2) the interval between the readings, (3) the degree to which the readings are to be integrated, e.g., by averaging over time and space, (4) the extent in time and space of the entire universe of observation, and (5) the criteria for significant change in the readings. In an observation set the concern is not just with system configurations frozen in a set of encounters with the meter, but also with the dynamics inferred from differentials between individual measurements.

Grain and Extent

Observation sets distinguish entities and levels by virtue of the surfaces detected. Two particularly relevant aspects of observation sets at this point are grain and extent, both of which position the observation set with respect to surfaces.

Grain determines the fineness of the distinctions that can be made in an observation set. Sampling more often or employing an analytical procedure that preserves fine distinctions, both make the observation set more fine grained. Lower level entities can only be seen in a fine-grained observation set which preserves the fine distinctions needed to discriminate between small things. Thus, in a time series, sampling intervals must be kept short to detect high frequency behavior. Grain determines the lower limits of observation and fixes the finest possible level of resolution in an observation set.

In contrast, extent determines the largest distinctions (i.e., the largest surfaces) that can be seen. If the characteristic behavior of a relevant large entity takes longer to occur than the period of the entire sampling regime, then the behavior can not be seen. Sampling for one summer season does not allow a plankton ecologist to address phenomena associated with the annual cycle. The difference between successive summers can only be studied if the observation set is extended to cover two or more summers. Sampling for only one summer fixes the extent so as to deny access to annual phenomena no matter what the mode of analysis.

The detection limits imposed by grain upon the smallness and, by extent, upon the grandness of phenomena are absolute. It is not possible to go beyond these limits once the observation set is fixed. Analysis and interpretation may impose further limitations even if the sampling aspects of grain are small and the extent is large. Understanding involves rejection of the full set of ways to look at a sampled system, in favor of a powerful subset that allows relevant prediction. It is precisely because of limits of human comprehension that analyses are performed explicitly to remove fine-grained distinctions so that large scaled phenomena may emerge in interpretation. The preliminary sampling aspects of grain and extent in observation sets give the limits of what it is possible to see; within these limits, transformation and analysis further confine what is seen to something commensurate with human comprehension. Furthermore, even with modern computers and a defined system like the game chess, computational limits are reached remarkably quickly (Pattee 1973). In systems where the rules are unknown, such as the interrelationships of the leaves on just one tree, computational limits close in immediately (Weinberg 1975).

Looking In and Out

Now consider the difference between looking in at entities as opposed to looking out at the environment. Looking inward, the observer sees the discreteness of entities (figs. 2, 3, and 4). Looking outward, the observer focuses his attention on the background rather than on any discrete object (figs. 5 and 6). Looking out directs attention at the environment, not the discrete entities.

Koestler (1967) emphasized the part-whole duality of entities in a hierarchical system. He viewed entities as windows of interconnection between their parts and the rest of the universe. Note how, in that conception, the rest of the universe is undifferentiated; it corresponds to our notion of environment. Looking out at the environment, in the present scheme, endeavors to fit the entity of interest into the larger whole. The entity is conceived as a part. By contrast, looking in toward its outer surface, the entity is seen as a whole.

Consider looking in, with an observation set of small extent so that only a single entity can be differentiated (fig. 4). Everything else is considered to be part of the environment. Environment is explicitly not differentiated into entities. It is that "everything else" which can be defined only in terms of its dynamical influence on the structures of definition. Now, increase the extent so that a second entity is detected and seen to be interacting with the first (fig. 3). Now a part of the original set of "environmental influences" can be seen to be interactions between the two entities. If structure is recognized in the environment, then one is no longer looking at environment, but instead, at a pair consisting of the original entity and the new entity which emerged from

the environment. The new structure emerged from the dynamical background as the extent of the observation set is increased. Looking outward focuses on the fact that the original entity, and now the pair of them, is part of a greater whole, as yet structurally undefined, and subject to influences from that context.

To match the part/whole duality of the entities in a hierarchical system, there is a corresponding duality for dynamics. Dynamics link parts to make the whole and deliver the influence of the whole to the parts. Entities sandwiched between the dynamical influences of their environment are in one direction, and the dynamical interaction of their parts are in the other direction.

Structures thus possess two sets of behaviors or processes. One set is directed upward to the next level and pertains to the "part" mode of the structural part/whole duality. The other behavior is directed downward, and is the dynamic that pertains to the "whole" mode of the structural part/whole duality. This downward directed dynamic gives the structure as a whole control over its parts. It is not always immediately apparent to which set (i.e., upward or downward directed) any given behavior belongs. That only emerges when grain and extent are manipulated for several criteria so that dynamics leading to parts can be discriminated from behavior leading to higher levels. It is possible for a given behavior to have aspects that lead upwards and other aspects that lead down, as will be demonstrated later.

Moving through Surfaces

When a surface is viewed from the outside, the separateness of the parts is ordinarily lost (fig. 4 compared to fig. 2). Conversely, when a surface is viewed from the inside, the separate identities of other higher level entities are lost (fig. 2). Distinctions that can be made on one side of the surface cannot be made on the other, because the signal is integrated and filtered out by the surface. The separate parts are merged into the integrated whole (fig. 4) and the other entities are mere-

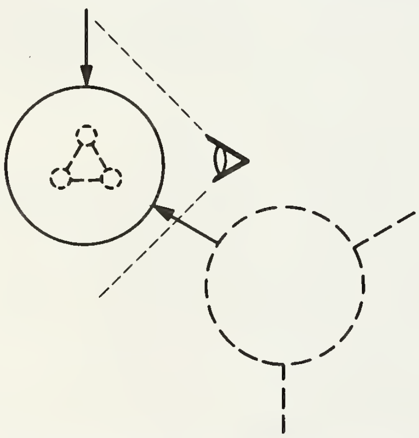

Figure 4.—Seen from outside, the parts are obscured by the intervening surface and the other entity is manifested only as an environmental influence of undefined origin. (The eye indicates the position from which the system is observed.)

Figure 5.—From inside the surface, looking outward, the observer cannot see the other entity because of the intervening surface. All he can see are the wavy lines which denote environmental influences modified by the surface. (The eye indicates the position from which the system is observed.)

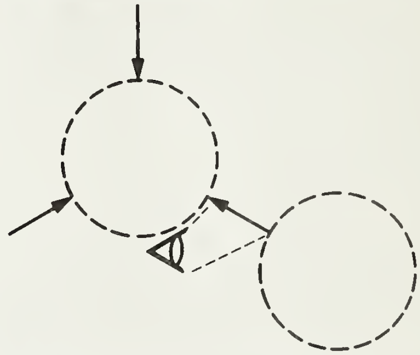

Figure 6.—When the observer looks outward from a surface, he can identify unmodified environmental influences, but he does not have sufficient scope of vision to see the other entity. (The eye indicates the position from which the system is observed.)

ly part of an undifferentiated environmental influence (fig. 5). In both cases, structure on the other side cannot be seen through the surface (Platt 1969). When an observer moves far enough through a surface, the distinctions on the other side become clear. Either formerly obscure parts can be detected (figs. 2, 4, and 5) or separate entities emerge from the environment (figs. 2 to 6).

The way appearances and relationships change as one moves through a surface can be clarified by an example. Species association (Williams and Lambert 1959) is a relative matter, relative particularly to the size of the universe in which the comparison is made (i.e., the extent of the observation set). Consider a two-by-two contingency table for tree species association within a forest. Such a table might well show a negative association between species occurrences, indicating distinct distributions of the species within the forest. The association is negative, because most samples contain either one species or the other, and relatively few contain both.

Now increase the extent of the observation set with additional samples taken in adjacent grasslands. Because neither species appears in these new samples, the number of mutual occurrences does not change. Previously, expectations of mutual occurrence were high, because both species were common in the data set: common species should occur together commonly. As the observation set is extended, the proportion of

samples containing either species becomes smaller. As the species become less common, there should be fewer mutual occurrences, and the observed values move closer to expectations. As a result, the negative correlation disappears. Move out through a surface and the distinction between the species distributions (inferred from the negative correlation) is obscured (fig. 2 compared to fig. 4).

Further expansion of the observation set to include more and more grassland samples makes both species rare, and their mutual occurrences now appear higher than expected. That is, the two species are now very rare and generally would not be expected to occur together at all. However, they still do occur together: now more frequently than one would expect if each were randomly distributed across the entire sampling universe. At this point they become positively associated and are seen as sharing the status of "forest species." Now, positive associations appear among forest species, and negative associations separate the forest species as a group from the grassland species as a group (Beals 1973).

Moving out through the surface of the forest altered what can be observed. Within the forest (fig. 2) one could discriminate between species distributions. Pioneer trees were distinguished from climax trees by negative associations (i.e., if one is present, the other is likely to be absent). As the observation set is expanded, the distinction between species (fig. 4) is lost. Pioneer and climax trees are both forest species, and that common identity begins to emerge. Further expansion of the observation set (fig. 3) makes it impossible to discriminate among tree species, which are now seen together as part of an entity distinguished from a second entity (i.e., grassland species) by negative associations.

Moving Out through a Surface

Movement out through any surface, such as the forest, is achieved through a new observation set which is greater in extent. Usually, it is also more coarse-grained. Coarse grain erects an opaque surface, because it does not allow perception of the smaller entities on the other side of the surface (fig. 4). Movement in through a surface may be achieved by the converse operations, using an observation set which has smaller extent and is also finer grained. The observation set now has a narrower extent, and the observer is trapped within the surface of any entity larger than the extent of the observation set (fig. 2).

Because of the change in grain, surfaces are ordinarily opaque. The only exception is when a new observation set involves only a change in extent. When a higher level emerges by virtue of a simple increase in extent, the smaller entities still may be detectable and are not necessarily obscured by the surface. It is this special case that allows one to tunnel from one level to the next, and to draw direct perceptual links between levels.

Transparent surfaces are crucial for linking levels, but are limited as a way to look at the higher level entity. When a surface is transparent, the new entity is simply an aggregate. It is being viewed by the same criteria which make the parts interesting objects of study. New properties which might be interesting at the higher level, sometimes called emergent properties, will not ordinarily be seen in this observation set. Higher levels of organization are important precisely because they have properties which are not immediately relevant to the parts. If organisms seen as aggregates of organs and tissues did not also display homeostasis and reproduction, there would be little reason to designate them as special objects of study. It is only when new properties are seen that the differentiation of the higher level entity advances understanding and enriches experience. These properties do not appear unless the criteria for observing the higher level entity differ from those used to study the parts. Thus, the observation sets appropriate for different levels ordinarily differ in criteria. Although there is a special case where surfaces appear transparent, the normal change in observation criteria that occurs as the observer changes his level ensures that the surfaces of most entities are opaque.

Returning through the Surface

Once the interesting properties of the higher level entity are identified, it is often profitable to change grain and extent and move back within the surface. However, now the criteria for observation have changed. For example, "forest" might be identified as a higher level entity in an extensive observation set on tree species. Now the interest is in the forest as an entity that fixes carbon. At this point the focus is on a new property of the forest. The motivation for moving back across the surface of the forest is to identify relationships or interactions (which may amount to mechanisms) operating between the parts, which explain the new property. The surface of the larger entity is transparent under this new criterion, since only extent manipulated and primary production by individual trees within the forest is observed. However, the new observation set on the lower level entities is based on new criteria and is not identical to first observation of this level. In the first observation set, trees were grouped into species categories. Now, when the observer re-enters the forest, entities may be grouped according to whether they are in the canopy or the understory, irrespective of species. New entities, herbaceous plants which were not considered in the original observation set, will also be included.

It is satisfying to the observer if the parts and their interactions in the new observation set are identical to those observed in the original analysis of the trees. In this case he feels confident in the linkage established between the levels. However, in the face of emergent properties, there is the possibility that the parts and processes observed by moving back inside the surface will be somewhat different.

If the same parts and processes cannot be observed as one moves back within the surface, the linkage between levels (i.e., between the new properties of the higher level and the old parts in the original observation

set) remains inferential rather that perceptual, and the surface is opaque. The point of significance here is that there is no reason to expect criteria for observing one level to apply to observing another. The only time a match can be hoped for is when only grain and extent are changed. When criteria of observation change (i.e., when new properties are identified at the higher level) there is no *a priori* reason to believe that the new properties can be reduced to interactions among the old parts. New parts and new processes may be expected. Just because large scale entities remain observable under new criteria (e.g., forest defined by carbon fixation rate as opposed to species composition), there is no need to expect a concomitant mapping (Rosen 1977) of the parts. The large scale entity may be robust (i.e., preserved under different observation criteria), even though the parts needed to explain behavior under the new criteria may change. The result is that trying to link properties of interest at one level to properties of interest at a different level is a difficult process.

Inferring the Whole from the Dynamics of the Parts

Despite the difficulties, ecologists must draw inferences across levels. Therefore, one must analyze what is involved in such inferences. With increase in the extent of an observation set, a surface is reached. At this point, a set of interacting entities have formed a sort of closure, so that they are interacting among themselves with high frequency and show only lower frequency interactions with the undifferentiated environment. The higher level entity has now emerged (fig. 7).

By comparing observation sets on either side of this surface, one can now infer that the entities observed inside the surface indeed are the interacting parts which make up the new whole and can be observed from outside the surface (fig. 7). It is precisely the rapid interactions among the parts which result in the structural integrity of this new whole. The new structure is defined by the dynamics of the parts.

Note here that multiple observation sets are required to draw inferences about linkages between levels. Observation sets that differ in criteria or in both grain and extent may only be linked by inference, because each is a separate mapping of the world. The closest one can come perceptually to link between levels is a change in extent, with every effort made to keep the grain and criteria for distinction the same. If criteria change, one cannot be sure of correspondence.

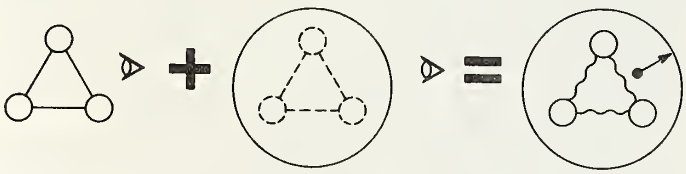

Figure 7.—Drawing inferences about the relationship between parts and wholes. The first observation set sees the collection of parts and their interactions but cannot see the larger whole because of narrow extent. The second observation set uses the same criteria for distinction, but with coarser grain and larger extent. This second set sees the whole but, at best, only a ghost of the parts. Together these two observation sets allow inferences to be drawn on how relationships among the parts lead to the whole. The dot-arrow symbol points to the whole, but the dot is within, because the whole is conceived as being derived from separate parts. The wavy lines denote inferred rather than perceived relationships.

Inferring Environmental Filtering

Moving through a surface while focusing attention outward (i.e., on the environment) leads to a completely new situation (figs. 2 to 5). Now inferences are sought about the manner in which the whole modifies the experience of its parts by filtering of environmental influences. Because the focus is not on entities, the required change in observation set can seldom, if ever, be made by a simple change in extent. The situation will ordinarily involve at least two observation sets and an inference drawn from the comparison (fig. 8).

There is a significant difference in the environment viewed from inside (fig. 5) and outside (fig. 3) of the surface. Outside, an undifferentiated background is seen as influence, manifested in the behavior of the whole through its correlation with environmental measurements. Environmental influence on the parts cannot be perceived, because the parts themselves cannot be seen (fig. 3). Inside, one can see environmental signal modified by passage through the surface. Comparing the observation sets one can infer that the whole modifies environmental influences before they operate directly on the parts (fig. 8).

An example here might help clarify the point. Consider diurnal temperature fluctuations and a forest. Outside the forest, temperature fluctuations are quite large. Inside, the biomass of the trees moderates these fluctuations. Forest trees experience cooler temperatures during the day and warmer temperatures at night than a single tree standing alone in a field. The forest tree experiences only the modified influence, and it is beside the point that the night temperature outside the forest is low. Thus, it is by drawing an inference from the observation of the temperature inside and outside the forest that it can be stated that the environmental influence is modified by the forest. Only then can the observer conclude that the temperature difference results from the moderating influence of the forest, which filters the temperature signal from the environment. In general, in order to draw conclusions about the role of the whole in modifying the environment or constraining the parts, a procedure like this must be followed.

Drawing Inferences Versus Changing Extent

Ecologists often draw inferences using observation sets based on different criteria. There is an important difference between crossing a surface by manipulation of grain and extent, and crossing by change of criteria. When grain and extent are changed to give a different pattern but the criteria for distinction are held constant,

then an orderly change has taken place. The parts and whole are linked in the change that took the observer through a surface. When a change occurs by the imposition of different criteria, the observation sets represent different mappings of the world. It may be that there is coherence across the change, and indeed the change does reflect a part/whole relationship, but this is not necessarily the case.

It should be apparent that errors could easily be made whenever the observer unwittingly changes the criteria for significance. A case in point could involve drawing inferences between species composition of a forest and nutrient cycling. Reduction of grain and extent in an observation set on the forest may show the system parts not as species but as functional entities. These entities may be formed by the interaction of soil, water, organic matter, parts of some plants (root hairs), all of some fungi (mycorrhizae), and communities of organisms such as microbes and nematodes that migrate in and out and are not always included in the functional part. The community with its species will not reappear. As a result, inferences drawn between species composition and the components of nutrient cycling must be tenuous, at best.

Often such inferences can be made more explicit by comparing observation sets that differ only in grain and extent. A case in point arises in comparing ordination analyses based on different criteria. Focusing on different phenomena reveals different aspects of the community. Each aspect refers to organismal relationships based on some linking factor such as disturbance, soil moisture, or intensity of competition. Different factors are based on different criteria of observation, and give constellations of species relationships that reflect different scales in time and space.

As an example, it is possible to interpret communities as determined by either competition or environment. By focusing on competition over a narrow range of mesic conditions, environment becomes merely the context within which competition occurs. On a larger geographic scale which includes environmentally stressed sites, one can view environment as the direct cause of species distributions (Allen and Starr 1982). The difference between the two emphases can be seen, for example, in the way that the tolerant, poor competitors (i.e., losers in one observation set) occupy stressed sites successfully (i.e., winners in the other observation set). Notice how it is difficult to hold these two concepts of community at the same time; for environmental stress is the frame in one, whereas competition is the frame in the other. Furthermore, competition is explicitly irrelevant in the stress frame. Putting it another way, a view that focuses on one set of phenomena cannot give a perfect account of a system if the interest is in some different set of phenomena.

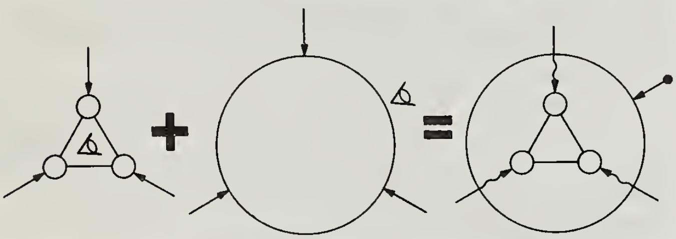

Figure 8.—Drawing inferences about environment based on two observation sets. The first observation set sees only the parts and their immediate environmental influences. The second observation set considers the whole as itself a part of some undifferentiated higher level. Together, these two observation sites allow inferences to be drawn about how the whole ameliorates the environmental experience of the parts. The dot-arrow symbol points to the whole and the dot is outside since the whole is conceived as a modifier of the environmental influence coming from the outside. The wavy lines denote inferred, not perceived, relationships.

To look at a specific case, Loucks (1962) performed ordinations of forests in New Brunswick by two different criteria. One was a Bray and Curtis (1957) ordination of stand species composition. The other was based on scalars of environmental gradients. This is a clear case of change of criteria. Because of this, Loucks was forced into an extended and deeply inferential argument to relate the results of the two ordinations.

The difference between the ordination results was great in that the moisture gradient curved around in the vegetation analysis. Black spruce and cedar were positioned together in the vegetation ordination at the ends of the distorted moisture gradient. In the environmental ordination, the moisture gradient must necessarily be straight, and black spruce and cedar are bimodally distributed, appearing at either end in very moist or very dry sites.

While Loucks was forced to explain these changes indirectly, he recognized that a series of observation sets of increasing extent would be a more direct approach:

"The data for black spruce suggest that if the samples in the lowest [stressed] range of the Nutrient scalar were considered alone, black spruce is not bimodal. It becomes so only when considered with preponderence of other communities that develop at higher levels of the Nutrient scalar; these nutrient levels occur only on intermediate moisture positions." (Loucks 1962.)

If he had begun with the low nutrient sites and expanded the extent to include more and more mesic sites, he would have seen black spruce and cedar change in an orderly fashion. Both low nutrient status and wet/dry extremes of the moisture gradient represent environmental stress. At the extremes, abiotic stress allows survival of the tolerant in a circumstance where competition is unimportant. Black spruce and cedar would have become rare as the number of mesic sites increased, because neither of them do well under mesic conditions, where competition with other species is important. Then the fine-grained concept (i.e., structured by competition) and the coarse-grained concept (i.e., structured by environment) could have been directly related through a simple change of grain and extent.

Correct and Incorrect Linkages

At this point ecologists can begin to identify the types of error they encounter when endeavoring to link levels of organization. Some rules and warning are already

part of ecological practice, having emerged from the exercise of common sense. Even so, there is something to be said for a scheme that derives from general principles instead of common practice. The former would be a general prescriptive scheme, the latter merely local and descriptive.

Linking Levels through Phenomena

Any scientific investigation starts by designating the entities one chooses to discriminate. The entities are structural and arise from the criteria for recognizing entities in an observation set. For example, one can choose to study individual organisms. Then he observes that the individuals demonstrate behavior (i.e., they can change through time). Once the entities are fixed, the observer has no choice as to whether or not his measuring device detects change. In this sense, the behavior of the individuals is forced on the observer.

Although the dynamics of the entities are forced on the observer, he must still make a second, observer-dependent choice concerning which specific dynamics he will consider to be of importance. The observer must enter the process again and decide the particular changes of state he will select as significant. The changes he selects constitute the "phenomena" of interest. Thus phenomena are dynamical behavior but are quite distinct from the raw dynamics that are imposed on the observer when he infers differentials for the measured states of the structure of interest. The raw dynamics are objective and imposed on the observer, while the dynamic which is a phenomenon is the special subjectively chosen subset which represents only the dynamics asserted to be interesting.

Observation, therefore, depends on two distinct choices separated by dynamics. The steps involved in setting up any observation set are (1) the choice of the level of interest and the entities or structures at the level, (2) the development of a means to observe changes in these entities, and (3) the choice of which changes will be considered significant (Rosen 1977). The observer decides about both entities and phenomena even though the dynamics are imposed on him.

Phenomena form crucial links between levels. Consider observations made on individual organisms through time (fig. 9). Among other things, the observer notices that eventually each of the individuals ceases to function. He decides this change of state is interesting, and "death" is established as the phenomenon (fig. 9). By increasing the extent of our observation set to include the death of many individuals it is possible to calculate a death rate.

The dynamic now links the observations to a higher structural level since death rate is a behavioral dynamic of the population (fig.9). The individual and the population are linked through their dynamics by having a phenomenon, death, in common. Whenever a phenomenon is significant at two levels, it can be used to link the levels. The link is made perceptually since it only involves changing the extent of the data set on dynamics. This is another example of the fact that a direct or perceptual

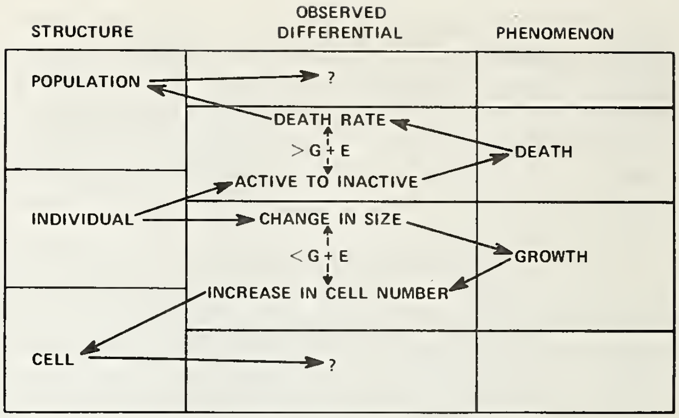

Figure 9.—Entities at structural levels above and below the individual are linked by first observing a differential (i.e., a change in state), then denoting an appropriate phenomenon, and finally observing again with modified grain and extent to observe a new behavior that links the phenomenon to the other level.

linkage between levels can only be made by a simple change in grain and extent while maintaining the same criterion of distinction.

An analogous path can be followed to connect the organism to lower levels (fig. 9). Once again observations will be made on the individuals, but now special attention will be given to change in size for each organism. Thus, "growth" is selected as the phenomenon. If the extent of the observation set is maintained, but a much finer grain is selected, changes in the number of cells might be seen (fig. 9). This leads to a lower structural level, because change in number is a dynamic definable on the entity, "cell." Thus, once again levels have been linked by a change in grain and extent using a phenomenon that they have in common. Note, however, that we could choose the phenomenon "growth," see trees grow, expand extent to see many trees growing, and then infer growth as an internal dynamic of a larger structure, namely forest.

Of course, it is possible to explain the phenomenon of growth in other ways. One might decide to examine caloric inputs, arriving at growth as the net difference. This approach is certainly legitimate, but, because of the change in criteria, it is unlikely that cells would be discovered as a lower level entity. The change in criterion would destroy the ability to link these levels considered above.

This approach for linking levels may seem pedantic and overdrawn. However, the necessity for the distinctions can only be appreciated when we see the errors which can be made when the linkage is made on less rigorous grounds.

Error in Linking Levels

The level to which the link is made may change depending on the phenomenon chosen. In the end, different levels may be linked than those the observer had in mind because the phenomenon chosen had different consequences than those he intended. The starting point for this example is the population, and the dynamic involves

foraging and eating. If the behavior, eating, is seen to be associated with the phenomenon, pollination, then an expanded conservation set could lead to an upper level entity called "guild" (fig. 10). Alternatively, given the same structure and behavior, if the phenomenon is recognized as primary consumption, then an increase in extent of observation set would lead to "trophic level." As a further alternative, recognition of the behavior as an interspecific relationship might lead one up the "community" (fig. 10). Thus, the linkages depend on the phenomenon, not just the raw observed changes in state.

Similarly, the levels which the ecologist links may change, if he changes the dynamics which he observes. Consider figure 9 once again; but now observe whether or not individuals mate with each other. The relevant phenomenon might now be constancy of mating among individuals of a similar type. Now a change in extent would not lead to the population or community, but to the taxonomic species as the next higher level.

These examples illustrate a problem commonly found in linking levels in ecology. Given the definition of level and phenomenon, it is clear from figure 10 that there are no absolute levels of organization, independent of the observer. There is no Platonic Chain of Being. Given a prior choice of structure defining the starting level, it is the choice of phenomenon that determines what is the next level in the hierarchy, whether it is the next level up or down. The phenomenon is chosen by the observer, not imposed by the external world; and it is the phenomena that both explain the workings of higher levels and describe the role of lower levels. Thus, the analysis presented here reveals that any attempt to find the true ecological hierarchy (e.g., MacMahon et al. 1981) is founded on an inadequate epistemological base and must of necessity fail. Intermediate or alternative levels always can be located by a change of phenomenon. When one moves up and down from the starting point of choice, the other levels are not fixed by what other investigators, with other observation sets, might choose as their starting points. Thus, the first problem with this analysis is the widespread practice of choosing the levels in the hierarchy *a priori*. The higher and lower levels must be revealed to the observer by a

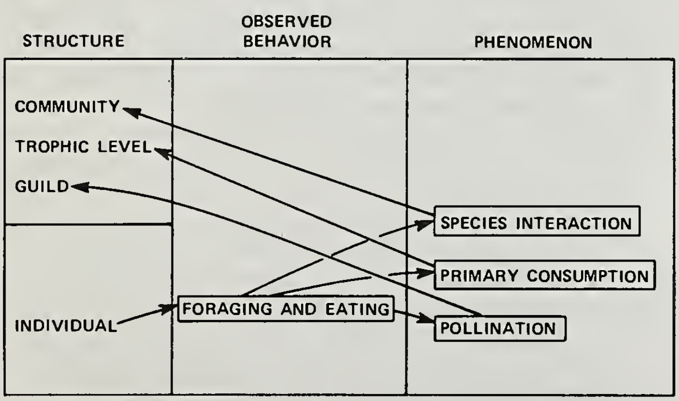

Figure 10.—The structures at the individual level are observed to change state and so exhibit behavior. Three different phenomena can be chosen on the same observation set and each links the individual level with a different upper level structure.

change in grain and extent with the entities needed to explain the mechanics (lower) and function (higher) of the chosen phenomenon.

This problem often arises in linking levels which are widely separated. Allen and Starr (1982) note that it becomes much harder to connect levels directly when there are intervening levels which are relevant to the chosen phenomenon but ignored. A case in point would involve explaining environmental control of phytoplankton communities by recourse to cell physiology and uptake rates of nutrients. Allen at al. (1977) suggest that the intervening levels of species, guilds, and strategies (Allen and Koonce 1973) attenuate and confound the linkage. Difficulty arises because the levels of observation are too far apart and articulation is lost. The levels of organization were imposed instead of being allowed to emerge from observations.

A similar problem arises in attempts to link ecosystems to communities or populations (fig. 11). Once again, the levels are prescribed, and the linkage is assumed. It is true that ecosystems have populations in them, but this "observation" actually involves a number of observation sets, based on very different criteria. In this report, it has been demonstrated that such a specification of the complex problem is inadequate, and depends upon insufficient evidence to establish the linkage. As a result, there is an epistemological problem with defining the ecosystems as composed of plant and animal populations and their environment.

To link ecosystems and populations, it is necessary to establish common phenomena and show that the observation sets that lead upward to the ecosystem and downward to the population involve a change of grain and extent but not change in criteria. In fact, it is possible to make this connection for some phenomena but not for others (fig. 11). Consider, for example, primary production. Here, a simple change of grain and extent will reveal that plant populations, and nothing else, are involved in this dynamic. However, other ecosystem phenomena, such as nutrient retention, do not provide adequate linkages. It was previously identified how a relevant component here, the rhizosphere, is a strange mixture of organism wholes and parts. The problem is that the dynamic does not result only from interactions among biotic populations. Nutrient retention may be in part biotic (tree boles), it may be abiotic (soil organic matter), or it may be due to a complex interaction. In this case, the ecosystem dynamic will not emerge from any observation set on the populations and their interactions. There is no simple increase in grain and extent that takes the population observations to nutrient retention dynamics of the ecosystem. The links only occur when an ecosystem phenomenon is given account by a single population or an aggregate of populations.

Another common error in linking ecological levels results from ambiguity in the words used to delineate a phenomenon. For example, the word "competition" implies a link between individuals and populations. However, the meaning to the word is verv level-dependent. As Harper (1967) points out, individual competition is commonly between the mature of one species

and the juveniles of another. Therefore, there is much confounding of neighborhood and population competition. Although the treatment of competition as something very local permeates much of J. L. Harper's earlier work, "Neighborhood competition" did not even arise as a specific technical term for individual to individual competition until recently (Mack and Harper 1977). The taxonomy of the individuals in neighborhood competition is usually unhelpful in explaining the observation since size and maturity are the determining factors. At the population level, "competition" refers to interactions among populations. Thus, if the observation set used to detect neighborhood competition does not contain information on the species, it cannot be changed by grain and extent to detect the competition which is of interest at the population level. If the observation set that detects population competition does not (as most do not) contain size hierarchy information, then a narrowing of grain and extent will not lead to neighborhood competition. The relationship between the two types of competition is by metaphor or, at best, analogy. The mistake is to assume that they are homologous.

Neighborhood competition viewed as resource capture does lead to populations seen in terms of resource base, because behavior of populations with respect to resource base is a simple extension of neighborhood resource capture, that extension being achieved through manipulation of only grain and extent. It is a population behavior that may be seen as directed downward. Population competition, however, involves behavior that is most readily seen as linking populations to make higher, not lower, hierarchical levels.

Similar ambiguities arise with the word "stability" used to link ecosystems and populations. At the ecosystem level, stability may refer to the constancy of a function, such as a primary production. At the population or community level, stability may refer to the fact that all of the populations are still there following a disturbance. However, it is quite possible the primary production has remained constant following a disturbance precisely because of species replacement resulting from resource competition. One population has disappeared and another has expanded to take over its function. Thus, the system can be considered simultaneously as stable and unstable depending on the level of interest. As a result, the phenomenon "stability" is a poor candidate for linking the levels. Simply because the same word is used for phenomena on two levels does not insure adequate linkage. One must be certain that the criteria have not changed even though the word has remained the same.

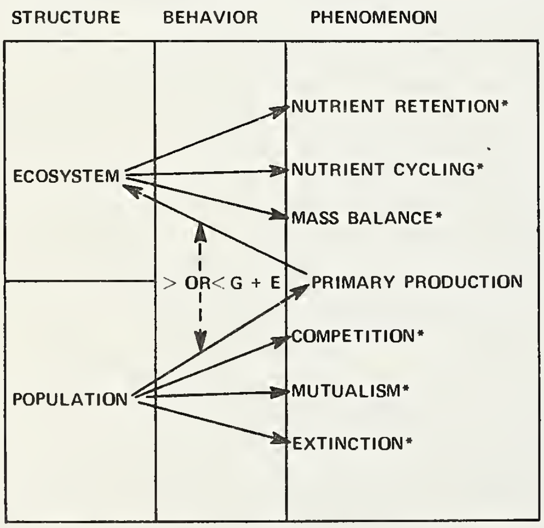

Figure 11.—Ecosystems can be linked to population, but only if a phenomenon can be identified that is common to both, such as primary production. The asterisks denote phenomena that are not common to both levels and cannot serve to link the levels.

Summary: General Principles for Linking Levels

The following summarizes these analyses in a set of general principles.

1. The level at which an inquiry begins is arbitrary. The observer chooses the entities on which he will focus and they are differentiated by observer-defined criteria. Effective criteria emphasize surfaces that (1) coincide with significant changes in rates of interaction, and (2) can be detected in different observation sets (i.e., are robust under transformation, as forest edges that coincide for change in both temperature and biomass).
2. A scientific description of the level chosen for study requires explicit recognition of part/whole duality (Koestler 1967). The entity of interest will consist of parts (i.e., lower level entities) which it constrains and contains. At the same time, the entity of interest must be seen as part of a greater whole, although this may be described in undifferentiated terms as its environment. To describe the entity as both a whole composed of parts and as a part of a greater whole will ordinarily require drawing inferences based on different observation sets; and the inferences will only be validly grounded on a perceptual basis if the criteria for significance have not changed between the observation sets. To move upward in the hierarchy will require an observation set with sufficient extent that it includes a number of entities and their interactions. To move downward requires an observation set of sufficiently fine grain that the individual parts and their interactions can be observed.
3. Once the observer begins to make observations on the entities, he can detect changes which correspond to their behavior unique to that level. A full description of dynamics, like structure, is also dual, and both delivers constraints downward to parts, as well as showing how the entity responds upwards to the greater whole of which it is a part. To understand both the upward and downward aspects of dynamics will ordinarily require inferences based on multiple observation sets.
4. Following observation of dynamics, a further observer-dependent choice must be made. This arbitrary decision involves the aspect of dynamics which will be given special significance and called

the "phenomenon" of interest. The choice of phenomena will then determine the higher and lower-level entities with which we can establish linkages.

5. Dynamic linkages between levels are established through phenomena. If the phenomenon in combination with a change of grain and/or extent can be established as interesting at both higher and lower structural levels, and if it can be related to each of these levels through observation sets on dynamics that differ only in extent or grain, then the linkage is justified. Care must be taken that the word used to describe the phenomenon has the same meaning on both levels.
6. Linkages between levels using only a change in grain and extent are crucial for established unequivocal or at least justified assertions of relationship. Only one phenomenon should be involved with only one set of criteria for observation. The relationship is simple because upper levels here are only aggregates of lower levels.
7. The simplicity of relationships so defined severly limits what insights can be derived. Fortunately levels which emerge from such simple relationships may persist when criteria for observing them are changed. Once they are found, emerging levels may be robust under transformation. Reverse manipulations of grain and extent using these new criteria do not usually lead back to the original level because a new phenomenon associated with the new criteria has become involved. Explanations of the new phenomenon do not return to the original level of concern but to a new level defined by the new criterion for observation.
8. From the above, the relationship between levels can be explained by alternative criteria (e.g., the relationship of a forest to alternative lower levels is complex: First, move from one lower level to a forest using one criterion, increasing the grain and extent; next, shift the criteria for defining a forest; finally, reduce to the alternative lower level by a reduction in grain and extent of the second criteria).
9. Attempts to link prescribed levels are difficult because the linking phenomena are undefined, and it may not be possible to find them under any observation set.

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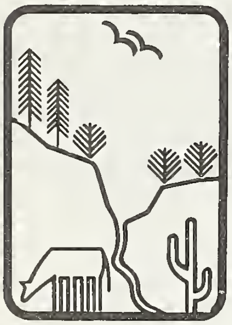
Rocky
Mountains



Southwest

Great
Plains

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